ON VARIATION OF THE ROSTRUM IN PALÆMONETES VULGARIS HERBST.

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LAST summer, at the Cold Spring Harbor Biological Laboratory of the Brooklyn Institute, I investigated the number of rostral spines in 1050 shrimps, in order to test the relation between the average value of a varying character and its variability.

As is well known, Verschaeffelt ('**94**) first assumed the ratio between the probable deviation of a character and its median to be an absolute measure of its variability. Such ratios as probable deviation or median average deviation, or root of average square deviation to mean have been called "coefficients of variation" and have been frequently used, not only in merely arithmetical processes, but also in dealing with morphological questions; for instance, in applying them, Brewster ('**97**) and Field ('**98**) meant to show the variability of systematically important characters to be higher than that of other ones. Both Davenport (see Brewster ['**97**]) and Pearson ('**97**) believe the higher variability of homologous characters to be connected with the higher average value. Dr. Davenport, to whom I am much indebted for his kind interest and for numerous suggestions during my stay at Cold Spring Harbor, assumes the relation between the index of variability of a character and its average value to be similar to that between the errors of measurement and the length of a course measured by the chain used in surveying.

Now, in my opinion ('**99**), there is no relation whatever between the average and the variability of a character. While the average value is determined by such conditions as equally affect all the individuals of a form unit, external conditions (environment, climate, food, quality of soil or water), as well as constitutional conditions (specific nature, sex, stage

of development), the variability depends upon numerous minute positively and negatively acting causes, a part of which only affects, in each case, the simple individuals of form unit in different combinations. Then the relative frequency of the individual variants in a form unit corresponds to the possibility of these combinations. Therefore, the causes of variation are to be thought of as essentially different from the conditions determining the average value of a character in the total form unit. On the other hand, I assume a relation between the morphological and physiological peculiarity of the different characters and the causes of their individual variation, so that the single characters are only able to react on a part of the sum total of the latter; therefore, in allied species homologous characters ought to show similar indices of variability, but not necessarily equal average values.

In 1892 Weldon investigated the numbers of dorsal and ventral spines of the rostrum in 915 individuals of *Palæmonetes varians* Leach from Saltram Park, near Plymouth, England. When I learned from Dr. Davenport that these numbers are markedly higher in the closely allied, if not identical, species, *Palæmonetes vulgaris* Herbst, at Cold Spring Harbor, I took up the investigation of 1050 individuals of the latter form in order to try, in at least one case, which opinion held true. If there existed any relation between average and variability, the latter ought to be sensibly higher in *P. vulgaris* than in *P. varians*. If I was right, the variability of the number of rostral spines, in spite of the higher average in *P. vulgaris*, ought to be about the same in both species.

I shall follow Weldon and deal with the males and females together, for among the 1050 individuals caught in the seine, only 92 were males. The males are much smaller than the females. The empirical results obtained from *P. vulgaris* are given in a table of combinations, those of *P. varians* (for comparison) in series of variations.

Explanation of letters used in the tables:

f, empirical, *y*, theoretical frequencies; *n*, total number of individuals investigated; Δ, error between empirical and theoretical series of variation in percentages of *n*; *A*, arithmetic

TABLE I. — COMBINATIONS IN PALÆMONETES VULGARIS

Dorsal spines		0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	*Palæmonetes vulgaris*	*Palæmonetes varians*
Ventral spines	0				1	2	1	1	2								7	3
	1						1	2	2	1							5	276
	2							1	15	31	8	1					57	630
	3							4	79	513	287	36					919	6
	4								1	21	28	7	1		1		59	$n = 915$
	5												1	2			3	
Palæmonetes vulgaris	*f.*				1	2	2	8	99	566	323	44	2	2	1		$n = 1050$	
	y.			.1	.2	.7	2.7	14.5	106.2	548.2	330.0	40.8	5.3	1.0	.3	.1	$\Delta = 1.63\%$	$\Delta\sqrt{n} = .5297$
Palæmonetes varians	*f.*		2	18	123	372	349	50	1	$n = 915$								
	y.	.1	1.7	18.3	122.2	374.6	345.9	51.7	.5	$\Delta = .31\%$ $\Delta\sqrt{n} = .0949$								

TABLE II. — CONSTANTS OF VARIATION.

	P. VULGARIS.		P. VARIANS.	
	DORSAL SPINES.	VENTRAL SPINES.	DORSAL SPINES.	VENTRAL SPINES.
A	8.2819	2.9781	4.3137	1.6984
ϵ	.8145	.4477	.8627	.4799
M	8.3079	3.1391	4.4634	
G	8.2395		4.2158	
δ	.8379		.9137	
a	1.4666		4.5457	
m	3.1260		42.2128	
τ	.2357		114.5962	
yo	623.86		.212733–25	
V	8.3632		10.6333	
$c.v.$	9.83%	15.03%	20.00%	28.26%

mean ; ϵ, index of variability = root of average square deviation from arithmetic mean ; M, mode = abscissa of maximum ordinate (ym) of the theoretical curve ; G, geometric mean ; $\delta = \sqrt{A^2 - G^2}$ (see Duncker ['**99**], p. 38) ; a, standard dimension of abscissa ; m, τ, exponents ; yo, ordinate of origin of theoretical curve ; θ, abscissa to yo ; $c.v.$, coefficient of variation = $100\,\epsilon : A$.

The theoretical curves, the polygons of which are represented in Pl. I, *C*, *D*, by dotted lines, belong to type IV, Pearson ('**95**) ; they are of the form,

$$y = yo\,(\cos\theta)^{2m} e^{-tg\,\theta},$$

where $tg\,\theta = \frac{x}{a}$ x means deviation from θ, and have been calculated by the method A (moments not modified) of Davenport ('**99**).

From this table we get the following results. The dorsal spines are much more numerous in both species than the ventral ones, and their variability is 1.8 times higher than that of the latter. The mean values of the homologous characters are about twice as large in *P. vulgaris* as in *P. varians;* nevertheless, the indices of variability are nearly equal in both species, in *P. vulgaris* even a little lower than

in *P. varians.* Judging from the coefficient of variation, however, we should find the numbers of ventral spines more variable than those of the dorsal ones, and the homologous characters only half as variable in *P. vulgaris* as in *P. varians.* Thus the coefficients of variation give quite different results from those obtained from the indices of variability, and only the latter ones, as Pl. I shows, correspond to the real conditions of variation in the four characters compared. *Therefore, in our examples, the indices of variability alone, not the coefficients of variation, are morphologically significant, and the former are similar in homologous characters, but independent of their mean values.*

The numbers of dorsal spines vary regularly, according to type IV of Pearson ('95) in both species with negative asymmetry of the variation curves, that is, the modes are higher than the means. It is remarkable that the ordinate of origin of the curve of *P. varians* lies at 10.63 of the abscissa, even higher than the mean and the ordinate of origin of *P. vulgaris.* Since both species, wherever they occur, are represented by immense numbers of individuals, their range of variation in the character considered probably extends much farther than will be expected from the empirical results of the investigations made by Weldon and myself. The variation curve in *P. vulgaris* is more symmetrical than that of *P. varians,* according to its small t-value. In both cases the agreement between the empirical series of variations and the theoretical one is thoroughly satisfying, the area of error between their two polygons remaining far behind its allowed upper limit,

$$\Delta\% = \frac{100}{\sqrt{n}}.$$

The numbers of ventral spines vary irregularly, which may partly be due to their small variability. In *P. varians* we find a curve of type I (asymmetrical, limited to both sides), where, however, the value $5\beta_2 - 6\beta_1 - 9$ is negative,[1] and where, accordingly, the index of asymmetry of this curve has a different sign from its third moment about the mean. In

[1] For explanation of these symbols, see Davenport ('99), or Duncker ('99).

P. vulgaris we get a curve of type IV, showing considerable asymmetry of its slope, probably in consequence of the abnormal frequency of the zero variant, while the empirical polygon of variation apparently corresponds to a nearly symmetrical curve. Of course there is no agreement between these curves and the empirical series of variation.

The correlation between the numbers of dorsal and ventral spines in *P. vulgaris* is positive, as is the rule in antimerically arranged homologous characters; its coefficient $r = .3878 \pm .0177$.

Besides variation in the number of spines there are some more individual differences in the shape of the rostrum of *P. vulgaris*, which will be seen from Figs. 2–27. The total rostrum may be compared with a knife, the blade of which is serrated on both edges, its handle bearing spines only on the back. In the spaces separating the spines there are feathered hairs in a single series; from the smooth ventral surface two rows of hairs extend from each side downward, like the rafters in a roof. In the males (Figs. 2–5) the rostrum is generally more slender and its handle longer than in the females (Figs. 6–27). While in *P. varians* Weldon found the apex of the rostrum bifid in more than half (52.8%) of all the individuals investigated, in our *P. vulgaris* it always was single-pointed.

With increasing numbers the spines stand together more closely and extend more forward to the apex of the rostrum (*cf.* Figs. 17 and 19 with Figs. 6 and 7); in case of very high numbers (extreme variation) they are sometimes irregularly arranged and of different sizes (Figs. 14–16, 18). Spines are rarely bifid (Fig. 13, third ventral), reduced (Fig. 20, between second and third dorsal; Fig. 21, behind first ventral) or entirely absent in a part of the otherwise normal rostrum (Fig. 22, between second and third dorsal). Very frequently, however, especially among the smaller numbers of spines, one meets with curious malformations (Figs. 5, 23–27), apparently due to regeneration, the rostrum, on account of its exposed situation, suffering easily from traumatic injuries. It would be interesting to learn if in the course of several moltings the

rostrum regenerates typically, that is, according to its individual variation of shape and of number of spines.

LITERATURE.

'97 BREWSTER, E. T. A Measure of Variability and the Relation of Individual Variations to Specific Differences. *Proc. Amer. Acad. Arts, Sci.* Vol. xxxii, No. 15, pp. 268–280.

'99 DAVENPORT, C. B. Statistical Methods, with Special Reference to Biological Variation. New York and London.

'99 DUNCKER, G. Die Methode der Variationsstatistik. *Arch. f. Entwickelungsmechanik.* Bd. viii, Nr. 1, pp. 112–187.

'98 FIELD, W. L. W. A Contribution to the Study of Individual Variation in the Wings of Lepidoptera. *Proc. Amer. Acad. Arts, Sci.* Vol. xxxiii, No. 21, pp. 389–395.

'95 PEARSON, K. Mathematical Contributions to the Theory of Evolution. II. Skew Variation in Homogeneous Material. *Phil. Trans. Roy. Soc.* Vol. clxxxvi, No. 153, pp. 343–414, 10 plates. London.

'97 PEARSON, K. On the Scientific Measure of Variability. *Nat. Sci.* Vol. xi, No. 66, pp. 115–118.

'94 VERSCHAEFFELT, E. Ueber graduelle Variabilität von pflanzlichen Eigenschaften. *Berichte Deutsch. Bot. Ges.* Bd. xii, Heft 10, pp. 350–355.

'92 WELDON, W. F. R. Palæmonetes varians in Plymouth. *Journ. Mar. Biol. Assoc. Un. Kingd.* N. S., Vol. 1, No. 2, pp. 459–461.

EXPLANATION OF PLATE I.

PL. I. Polygons of variation of numbers of spines; empirical polygons are given by continuous, theoretical ones by dotted lines.

A, ventral spines of *P. varians*.

B, ventral spines of *P. vulgaris*.

C, dorsal spines of *P. varians*.

D, dorsal spines of *P. vulgaris*.

ϵ, index of variability of polygon above.

ya, *ym*, *yo*, ordinates of theoretical curves to *A*, *M*, *O*, of abscissa; compare explanation of letters used in table, p. 624.

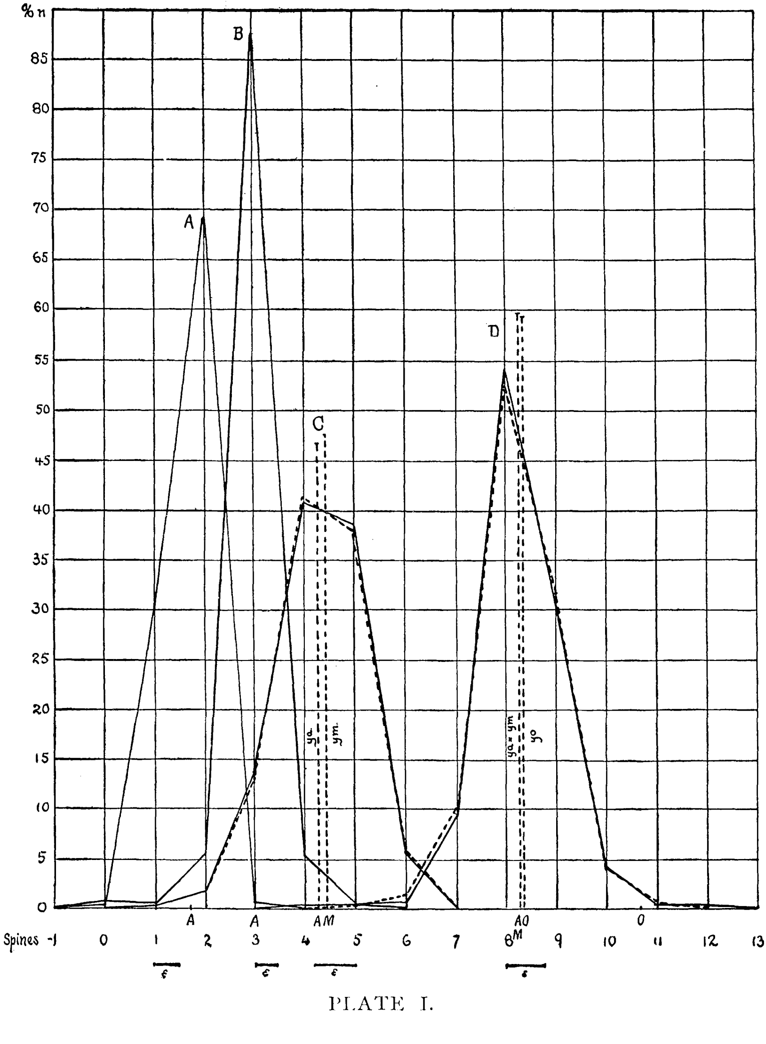
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PLATE I.

EXPLANATION OF PLATE II.

Camera drawings of rostra.

(Leitz, Oc. 1; Zeiss Obj. A,* II.)

FIGS. 2–5. Male rostra.

FIG. 2. Normal, 6 dorsal, 3 ventral spines.

FIG. 3. Normal, 9d. 3v.

FIG. 4. Irregular, 8d. 1v.

FIG. 5. Malformed, 5d. 0v.

FIGS. 6–22. Normal female rostra.

FIG. 6. Normal, 5d. 2v.

FIG. 7. Normal, 6d. 3v.

FIG. 8. Normal, 6d. 3v. (sixth dorsal broken).

FIG. 9. Normal, 7d. 3v.

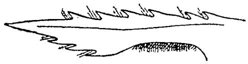
FIG. 10. Small irregularities in

FIG. 11. position of spines, 7d. 3v.

FIG. 12. Normal, 7d. 4v.

FIG. 13. Third ventral bifid, 8d. 3v.

FIG. 14. 10d. 3v. irregular position of spines.



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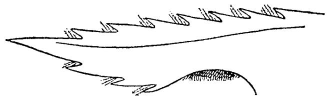

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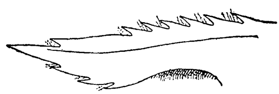

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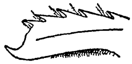

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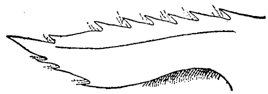

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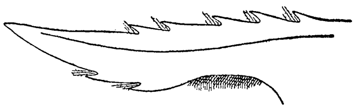

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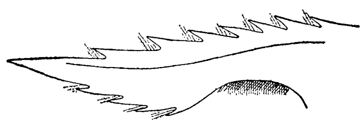

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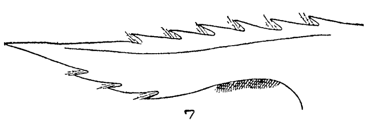

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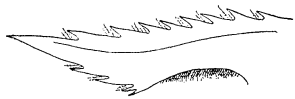

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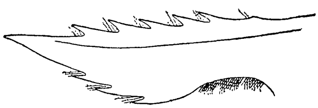

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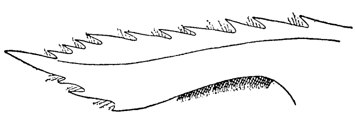

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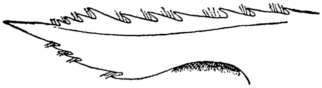
PLATE II.

EXPLANATION OF PLATE II (*Continued*).

FIG. 15. 10d. 4v. } irregular position of spines.
FIG. 16. 12d. 5v. }
FIG. 17. Normal, 12d. 5v.
FIG. 18. Irregular position of spines, 12d. 6v. (not in table ; found later).
FIG. 19. Normal, 13d. 4v.
FIG. 20. Some spines reduced, 6d. 3v.
FIG. 21. Some spines reduced, 7d, 1v.
FIG. 22. Some spines missing, 5d. 3v. (abnormally small).
FIGS. 23–27. Malformed female rostra.
FIG. 23. 8d. 3v.
FIG. 24. 8d. 3v.
FIG. 25. 7d. 3v.
FIG. 26. 6d. o(?)v.
FIG. 27. 4d. ov.



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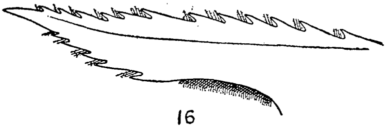

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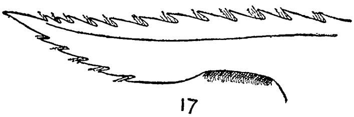

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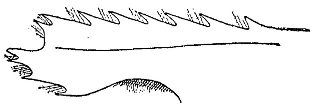

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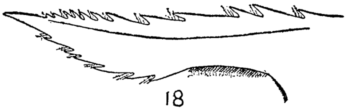

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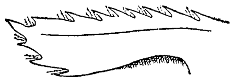

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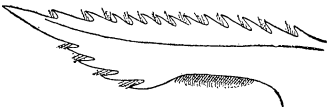

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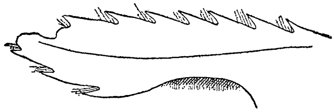

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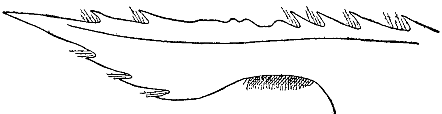

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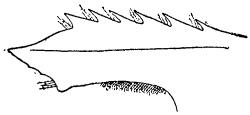

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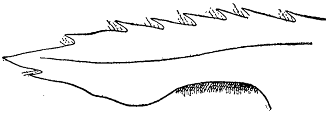

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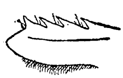

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PLATE II.